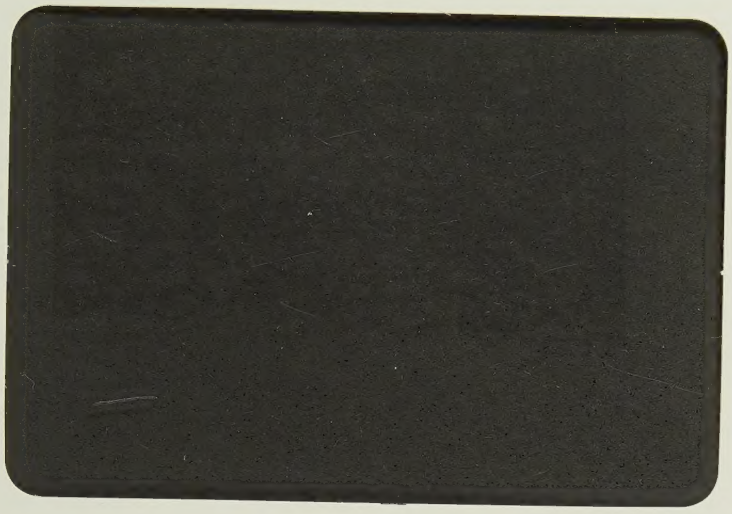

DEPARTMENT OF ZOOLOGY

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On the Feeding Ecology of Six Coexisting Gadoid Species in the Skagerak and the Kattegat

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This thesis is a summary of the following papers and they will be referred to by their Roman numerals:

I On the Feeding Ecology of the Cod, *Gadus morhua* L., in the Skagerak and the Kattegat. Manuscript.

II On Optimal Diet in Relation to Size of Cod, *Gadus morhua* L. Manuscript.

III On the Feeding Ecology of the Whiting, *Merlangius merlangus* (L.), the Pollack, *Pollachius pollachius* (L.), the Saithe, *P. virens* (L.), and the Hake, *Merluccius merluccius* L., in the Skagerak and the Kattegat. Manuscript.

IV On the Food Niches of Six Coexisting Gadoid Fishes in the Skagerak and the Kattegat. Manuscript.

INTRODUCTION

This thesis is based on four papers concerning the feeding ecology of the six coexisting larger gadoid species in the Skagerak and the Kattegat, namely cod, *Gadus morhua* L., Haddock, *Melanogrammus aeglefinus* (L.), whiting, *Merlangius merlangus* (L.), pollack, *Pollachius pollachius* (L.), saithe, *P. virens* (L.), and hake, *Merluccius merluccius* L.

Thus far, the models developed for the management of fish populations have been one-species models. A fish population is thought to be regulated by four factors, recruitment, growth, natural mortality and fishing mortality, all of which are treated as independant of other fish populations. This view is, of course, a conscious oversimplification.

Evidence from fisheries as well as from theoretical and applied ecology indicate that these one-species models are insufficient for the rational exploitation of fish stocks. Many of the species concerned are known to be predators of other species, and there are also indications of considerable competition.

During recent years the need for more comprehensive models has been recognized, and some investigations have been conducted in order to estimate the influence that different fish populations have on each other.

The main objective of the present investigation was to contribute to the knowledge of the diet of the larger gadoid fish species in the Skagerak and the Kattegat (I, III, IV). (These species are the most economically important demersal species for the Swedish fishery.) The food of the different species is described and information on predator-prey relationships among different species of fish is given. The possible competition among the gadoids is also discussed.

A secondary purpose of the investigation was to contribute to the theories of optimal diet and food niches (II, IV).

The following is a summary of the original papers to which the reader is referred for details and references.

On the Feeding Ecology of the Cod in the Skagerak and the Kattegat. (I)

The cod is by far the most common demersal fish in the Skagerak and the Kattegat and also the most economically important one for the Swedish fishery. The present study describes the feeding ecology of the cod in this area.

The stomachs of 1,419 cod collected by bottom trawling in the Skagerak and the Kattegat during September - April 1971-77 were analysed. The material was divided into three parts; 1) from the soft bottoms of the open sea 2) from the soft bottoms of the fiords and 3) from the sea-weed zone.

The cod feeds on a wide spectrum of prey; almost all types of organisms were found. Bottom-dwelling crustaceans dominated the food in the entire area and was present in more than 50% of all stomachs. Fish and polychaetes were found in fractions from about 15% to about 50% and molluscs, echinoderms and other food items in less than about 10%.

At least 24 species of fish occurred in the stomachs analysed. The most frequent species were Norway pout in the open sea and gobids and sprat in the fiords. These species were probably the most common fish species in the respective areas. (The material from the sea-weed zone is not adequate to permit the formation of any con-

clusions.) The fish prey were to almost 100% pre-recruited fish, of which a smaller part were commercially important species. The results suggest that predation by cod might have some influence on recruitment of other commercially important fish.

The most frequent crustacean was swimming crabs in the open sea, hermit crabs in the fiords and shore crabs in the sea-weed zone. These groups were probably the most common suitable crustacean prey in the respective areas. Shrimp was also frequent.

Aphrodite aculeata L. was the most frequent polychaete on the soft bottoms, but in the sea-weed zone, this species was almost absent.

There were minor differences in the general food pattern among the three subareas, the most pronounced one being the greater dominance of crustaceans in the open sea compared to the other areas. However, on the species level many differences were found, certainly to a large extent caused by differences in the potential food fauna.

The differences in the food within each one of the three subareas were minor compared to the differences between them.

The results showed that the cod seems to "adapt" well to different conditions, i.e. different food faunas.

Larger and more valuable types of prey were included in the diet of the larger cod. The fraction of fish increased, as did those of molluscs (mostly the large *Buccinum undatum* L.) and ophiuroids. The fraction of the large polychaete *Aphrodite aculeata* also increased. Within the crustaceans there was a gradual change from smaller to larger prey. Shrimp/euphausiaceans were most frequent in the smallest cod, hermit crabs in the slightly larger cod, crabs in the even larger, and Norwegian lobster in the largest cod. The probable explanation for these changes are: 1) It is advantageous (in terms of net rate of energy intake) to eat larger prey, and only the larger cod can capture these prey, and 2) fish have a higher nutritional value than e.g. crustaceans and are therefore favoured, and the larger the cod the greater its ability to catch fish. (See also II.)

There was a tendency for two feeding periods, at dawn and dusk. The reason is probably that many prey, in order to minimize the risk of being preyed upon, are active during darkness. This means that natural selection should favour the tendency of the cod for feeding during darker times of the day, and while feeding during complete darkness is difficult, feeding should be concentrated during dawn and dusk.

There was a tendency for a lower feeding rate just before and during spawning and a higher

rate just after spawning compared to other times of the year. The reason for decreased food intake during spawning could be that spawning and associated activities require too much attention and thereby supress the feeding activity to some extent. The increased food intake after spawning is certainly a means to regain the energy losses incurred during spawning.

On Optimal Diet in Relation to Size of Cod. (II)

Models of optimal diet and food niches have recently raised much interest.

The present study examines the diet of the cod in the Skagerak, focusing on changes in diet with variation in the size of the cod. It attempts to test the hypothesis that larger predators have wider niches. The material was also examined in the light of the "theory of optimal diet" in order to determine whether its predictions fit the present situation.

In the area considered in this investigation, the cod feeds mainly on bottom-dwelling crustaceans, of which swimming crabs dominate (I). Swimming crabs are therefore the major material of the present study (although the rest of the food was also considered) and the size of crab was studied in relation to size of cod.

The cod feeds on a wide range of food sizes. A widening food niche with increasing predator size was found for predators up to about 55 cm. This was caused by a considerable increase of the upper prey size range limit and a more or less constant lower one. For larger predators the food niche was roughly constant (or possibly slightly narrower), as the upper prey size range limit also becomes constant. However, although there is an approximately constant breadth of the food niche with respect to swimming crabs,

the results indicate that the food niche continues to widen for larger predators as well. Larger cod include larger prey (not available to the smaller predators) of other types in their diet, and if all types of prey were considered, the food niche probably widens throughout the predator size range. The fraction of polychaetes (a majority of which are the large *Aphrodite aculeata*), molluscs (almost exclusively larger *Buccinum undatum*) and ophiuroids increase with increasing predator size.

The reason the cod widens its food niche is probably that it cannot, while including larger prey (which are comparatively rare), make a corresponding exclusion of the smaller, more abundant ones. Feeding exclusively on the larger prey should mean a considerable increase in search time and consequently a decrease in net rate of energy intake. Thus, the smaller prey remain included in the diet.

With some minor reservations the theory of optimal diet could be applied to the present material. The three basic tenets of the theory were considered.

The fact that the smaller prey were included even in the diet of the largest cod suggest that larger prey are very rare compared to the smaller ones.

The maximum manegable prey size increases (i.e. food becomes more abundant) with increasing predator size. This is probably correlated with exclusion of the smallest prey, as predicted by the model of optimal diet.

While including larger prey, larger predators do not exclude the smallest ones completely. This seems to contradict the model, but is probably due to the fact that the actual foraging areas of the cod differed slightly in prey size distribution.

On the Feeding Ecology of the Whiting, the Pollack, the Saithe, and the Hake in the Skagerak and the Kattegat. (III)

The whiting, the pollack, the saithe and the hake are common fish species in the Skagerak and the Kattegat. The Swedish catches of these species together in the present area amounts to about three quarters of the catches of cod. The present study describes the feeding ecology of the four species in this area.

The stomachs of 400 whiting, 190 pollack, 391 saithe, and 395 hake collected by bottom trawling in the Skagerak and the Kattegat during September - February 1971-77 were analysed. Almost the entire material was collected in the open sea.

The whiting feeds on a wide spectrum of prey; almost all types of organisms were found. Demersal fish dominated and were present in well above 50% of the stomachs. Crustaceans were present in less than 50% and polychaetes in about 10%, while molluscs and ophiuroids were rare.

At least 8 species of fish were found. Gadoids dominated and Norway pout was the most frequent species.

The most frequent crustacean was shrimp. Swimming crabs and euphausiaceans were also common.

The pollack feeds predominantly on fish (present in well above 50% of the stomachs) and crus-

taceans (present in less than 50% of the stomachs), while polychaetes, molluscs and echinoderms were infrequent.

At least 16 species of fish occurred. Gadoids dominated, and Norway pout was the most frequent species.

The most frequent crustacean was shrimp.

The saithe feeds predominantly on fish (present in well above 50% of the stomachs) and crustaceans (present in less than 50% of the stomachs), while molluscs were rare and other groups not present at all.

Ten species of fish occurred in the stomachs analysed. Gadoids dominated, and Norway pout was the most frequent species.

The most frequent crustacean was euphausiaceans, but shrimp were also common.

The hake feeds predominantly on fish, which was present in almost all stomachs. Crustaceans were present in well below 50% of the stomachs, polychaetes and molluscs were rare, and other groups not present at all.

Fourteen species of fish were found. Gadoids dominated, and Norway pout was the most frequent species.

The most frequent crustacean was shrimp.

The four species feed to a large extent on fish (probably the most common species of suit-

able size). This indicates that although these species are less common than the cod (and as the cod to a large extent feed on commersially unimportant species), they could very well have some influence on the recruitment of other commercially important species.

With increasing size, whiting, pollack, saithe and hake change their diets and prey on fish to an even greater extent. The largest hake, for example, prey almost exclusively on fish. The probable explanation for this change is that fish have a higher nutritional value than e.g. crustaceans and are therefore favoured, and the larger the cod the greater its ability to capture fish.

The material was too small for a more in-depth analysis of the periodicity of the food intake.

On the Food Niches of Six Coexisting Gadoid Fishes in the Skagerak and the Kattegat. (IV)

Competition and niche theory have raised much interest among ecologists, and these issues have prompted considerable debate.

The present study attempts to describe the food niches of all six coexisting larger gadoid species in the Skagerak and the Kattegat, namely the cod, haddock, whiting, pollack, saithe, and hake.

The material consists of 614 cod, 400 whiting, 190 pollack, 391 saithe and 395 hake collected by bottom trawling during 1971-77 in this area. Data on the food of the haddock was taken from the literature.

Four different dypes of food niches emerged: 1) Cod, with a dominant fraction of crustaceans, supplemented by rather large fractions of polychaetes and fish. 2) Haddock, with almost equal fractions of echinoderms, polychaetes, crustaceans and molluscs. 3) Whiting, pollack and saithe, with a dominant fraction of fish supplemented by crustaceans. 4) Hake, with a diet consisting almost exclusively of fish.

Haddock has a food niche clearly distinct from the other species. The great majority of the prey of the haddock are not preyed upon by the other species.

The cod's principal prey (crabs and hermit crabs) are not preyed upon to any significant extent by other species. Thus, the cod also has a food niche which is clearly distinct from the other species.

The whiting, pollack, and saithe have similar food niches with regard to the main food groups. When analysed in depth, however, differences emerge with regard to both the fish and the crustaceans preyed upon. However, there are rather large food niche overlaps among these species.

The hake almost exclusively feeds on fish and has a food niche which completely falls within the niches of the whiting, pollack and saithe.

CONCLUSION

This study describes for the first time the food of the larger gadoids (except haddock) in the Skagerak and the Kattegat.

The present investigation shows that the feeding ecology of the cod in this area agrees in general with the earlier investigations from the north-east Atlantic area. This includes the main food groups consumed, the changes in food composition with changing cod size, and the periodicity of food consumption. There are, however, differences in the actual species composition of the food. These differences are certainly due to the differences in potential food fauna.

The food of the other species (of which only whiting has been investigated in depth) in the north-east Atlantic is also similar to that found in the present study.

The six species obviously have rather different food niches. Cod and haddock in particular have niches which are clearly distinct from the other species as well as from each other, both species being primarily bottom feeders. The cod feeds primarily on crabs and hermit crabs, supplemented by fish and the polychaete *Aphrodite aculeata*, while the haddock preys to an equal extent on echinoderms, polychaetes (other than *Aphrodite aculeata*), molluscs and crustaceans (other than crabs and hermit crabs). The whi-

ting as well is primarily a bottom feeder, but its principal food is fish. Pollack and saithe have diets which include more pelagic organisms, but bottom-dwelling prey are frequent as well. Fish constitute the principal food of these species also. Finally, the hake preys almost exclusively on fish, pelagic as well as bottom-dwelling ones.

One hypothesis states that the populations of at least some of these species are regulated during their first year of life. This implies that no competition should occur at later stages and completely overlapping food niches should be possible. The small food niche overlaps among some of the species studied, however, must be of some advantage, and competition could not, at this stage, be ruled out as an important factor.

All species (except haddock) prey to a considerable extent on fish, a great majority of which consists of gadoids, while a smaller fraction is composed of clupeoids. In the North sea the cod is probably exerting some influence on the recruitment of the other commercially important species. This means that these five species together probably have a significant influence on recruitment.

The present results show that cod from the Skagerak and the Kattegat feed on fish to a slightly lesser extent than the cod of the North

sea. Furthermore, a smaller fraction of the fish food is composed of commercially important species. The other gadoids prey to a greater extent on commercially important species, and also consume at least twice as much fish as the cod per individual.

This means that the larger gadoids of the Skagerak and the Kattegat together very well could have some influence on the recruitment of the other commercially important species.

In conclusion, the present investigation has presented valuable information on the food niches of the different gadoids, on their interrelationships, and on the relationships between them and other commercially important fish species. This study has also shown that the gadoids probably could exert some influence on the recruitment of other species and demonstrates the necessity of quantitative studies on the issue.

With regard to the theory of optimal diet, the investigation has also presented some field data which, although in accordance with the theory, demonstrate the diffeculty of applying the theory to field situations.

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I wish to thank Dr. Armin Lindquist for giving me the opportunity to participate in the expeditions of the research vessels of the Fishery Board of Sweden, and the crews of the fishing boats SD 121 Annika, SD 301 Monsun, LL 149 Björn, LL 301 Dover and GG 105 Titania for the opportunity to collect material on their expedtitions.

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